Lethal and Sublethal Predation on Cambrian Trilobites from North America

Undergraduate Research Thesis

Submitted in partial fulfillment of the requirements for graduation

with research distinction in Earth Sciences

in the undergraduate colleges of

The Ohio State University

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2019

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Abstract

Clarification of the criteria used to analyze broken trilobite exoskeletons increases the ease of distinguishing the origins of breakage. Detailed study of sublethal breakage shows that trilobites had the capability of healing sublethal wounds shortly after wounds were inflicted, and then regenerating lost tissue during subsequent molt stages.

Specimens from a variety of Cambrian deposits from North America were studied. Most trilobites were represented by fragmented remains. In some deposits, injuries are relatively common and these instances were studied in greater detail. Overall, the specimens show that injuries of uncertain origin are rare. Lethal predation injuries are rare as trace fossils on articulated specimens, indicating that many predators commonly macerated their prey. Compared to the number of uninjured trilobites, injuries in general were rare, showing that Cambrian predators were more often to have been successful than unsuccessful.

Among fossils showing sublethal predation scars, there appears to be considerable variability in the number of specimens showing such scars. Olenellines (Stage 3-Stage 4) had low incidences of preserved sublethal predation scars. Some Drumian Age taxa, such as Elrathia and Asaphiscus, have higher incidences of sublethal predation scars. Sublethal injuries on specimens of Elrathia kingii are preferentially preserved on the right thorax, which suggests that injuries in other areas were inflicted less often or more likely to prove fatal. Other common trilobites of the Drumian, such as Modocia, had preserved sublethal predation scars. This evidence suggests that some trilobite clades developed more efficient predation-resistant structures or behavioral strategies through time. Lethal predation or scavenging was commonly represented through the Cambrian Stage 3-Drumian interval by unhealed, broken sclerites, in coprolites, and in cololites. Incomplete, partly disrupted exoskeletons interpreted as scavenged remains are common in Cambrian Lagerstätten.

Acknowledgements

I would like to thank Dr. Loren Babcock for giving me this research opportunity and for being a mentor throughout my time as an undergraduate at The Ohio State University. I learned a lot about paleontology and making observations from him, especially regarding trilobites. I appreciate all of the time he took to advise me on graduate school, future career opportunities, and working to provide an exciting opportunity for continuing on to my Master's degree. I would like to thank Dr. Michael Barton for being on my thesis committee. I would like to thank Dr. Anne Carey for all of the time she took to provide resources and guide us through our thesis projects. I would like to thank Dr. Julie Sheets for guidance with and access to the Scanning Electron Microscope facility at Ohio State's School of Earth Sciences, as well as being a mentor and being willing to work with larger specimens in the SEM than she usually works with. A FEI Quanta 250 field emission gun scanning electron microscope at the Subsurface Energy Materials Characterization and Analysis Laboratory (SEMCAL), School of Earth Sciences, Ohio State for further study of some specimens. Studied specimens were left uncoated.

I would like to thank the Babcock Research Support Fund, Field Experiences Travel Fund from the School of Earth Sciences, Joan Echols Scholarship, and the Edmund Spieker Scholarship for providing funding for this project and for my education at Ohio State.

I'd also like to thank Rongqin Wen for taking the time to provide emotional support and advise me through the drama and challenges of finishing my thesis, all while trying to get her own thesis done.

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Introduction

Changes in predator-prey systems through the early and mid-Paleozoic are hypothesized to have played a major role in early animal evolution and in transforming ecological relationships in early marine ecosystems (Vermeij, 1987). Differences in interpretation of the evidence of carnivorous activity from fossils can lead to substantially different models of paleoecologic interactions. Paleoecology and evolution have mutually affected each other in the fossil record. Predation effects morphology, distribution, abundance, and evolution of metazoans (Babcock, 1993, 2003).

Evidence of predation or other injuries on trilobites extends to the earliest records of trilobites (Cambrian) through the Permian. Predation on and by trilobites probably influenced morphological and ecosystem development throughout the Paleozoic (Babcock, 1993, 2003).

Trilobites were a diverse group of arthropods in the Paleozoic, varying in size, life habits, and marine habits. They were prey for both large and small predators, who employed a variety of techniques in order to carry out this predation (Babcock, 2003).

Predator-prey interactions involving trilobites showcase important paleobiological issues such as the rise and development of Paleozoic marine predators, skeletization of metazoans during the early Paleozoic, wound response, internal organization, and lateralization of the metazoan nervous system. (Babcock, 1993, 2003, 2005)

Predation on and by trilobites is a subset of a larger reorganization of marine ecosystems, the Early Paleozoic Marine Revolution (Babcock, 2003), or EPMR, which was driven in large measure by escalation in predator-prey systems. The EPMR includes both the Cambrian Explosion and the Cambrian Substrate Revolution, both of which were influenced by predator-prey interactions. Reorganization or marine ecosystems extended to at least the late Cambrian.

Owen (1985), Babcock and Robison (1989), and Babcock (1993, 2003, 2005) discussed the classification and origins of malformations on trilobites. Collectively, these authors discussed the origins of injuries, where on the trilobite exoskeleton they are usually found, and their relationship to predators of trilobites. Babcock and Robison (1989), and Babcock (1993, 2003) showed that injuries are more common on the right side of the trilobite, as much as three times as common. The reason for the right side being more common is likely due to either predators preferring the right side or the right side being used in a way that allows the trilobite to escape. Pratt (1998) and Bicknell and Paterson (2018) provided further information about evidence of predation on trilobites, including broken sclerites.

Babcock (2003) gave an overview of predation on and by trilobites. He showed and explained the differences between various evidence of predation, such as scars, borings, gut contents of predators, coprolites, broken sclerites, and predation resistance or response. He discussed evidence and criteria for coprolites and gut contents of predators, as well as trilobites themselves, such as sclerites being found in the guts of predators and trilobites having fluid-filled guts. The key points of this paper for my research are showing how to recognize bite marks and how to distinguish them from other injuries, understanding the evidence for how predators of trilobites prey on them, understanding the implications of broken sclerites, and determining what constitutes a coprolite.

Babcock and Robison (1989) and Babcock (1993, 2003) documented the frequency of injuries on the right and left sides of trilobites. In all of these studies, differentiation was made between predation scars and injuries of uncertain origin. The researchers concluded that a tendency to side asymmetrical predation scars was related to brain laterality, similar to evidence of functional asymmetry in humans, and other species.

Robison et. al. (2015) is a good general reference to the Cambrian trilobites and opther fossils of Utah, and indeed the Great Basin generally. Coprolites and examples of healed bite marks are treated in the book.

Geologic Setting

Specimens studied were collected from various Cambrian strata in the Great Basin (Utah, Nevada, and California) and other regions of North America:

Figure 1. Localities of the specimens studied in this project are indicated with red stars.

Localities are summarized in the following list:

1. Campito Formation, Montenegro Member (Cambrian Stage 3), Esmeralda County, Nevada. Specimens were collected by Loren Babcock.

2. Poleta Formation, Middle Member (Cambrian Stage 3), Esmeralda County, Nevada. Specimens were collected by Loren Babcock.

3. Pioche Formation (Cambrian Stage 4), Ruin Wash, Nevada. Specimens were collected by the Gunther family. Specimens were collected by the Gunther family.

4. Kinzers Formation (Cambrian Stage 4), Lancaster County, Pennsylvania. Collectors of these specimens are not known.

5. Chisholm Formation (Wuliuan Stage), Lancaster County, Pennsylvania. Specimens were collected by the Gunther family.

6. Wheeler Formation (Drumian Stage), House Range and Drum Mountains, Utah. Specimens were collected by the Gunther family and others.

7. Marjum Formation (Drumian Stage), House Range, Utah. Specimens were collected by the Gunther family and others.

The taxa represented range in age from Cambrian Stage 3 to Drumian Age.

During the Cambrian, the Great Basin (Utah, Nevada, and California) was located on the northwestern margin of Laurentia. At the beginning of the Cambrian, the area was a coastal to shallow subtidal environment. A shallow sea, full of organisms, covered eastern Nevada. A shallow sea covered the Great Basin as the Cambrian proceeded, complete covering it by the end of the period. This sea level rise was likely due to an increased formation of thermally expanded crustal rock along seafloor spreading ridges, in addition to other factors (Robison, et. al., 2015). Babcock et al. (2015) also discussed glacio-eustasy as important in Cambrian sea level history.

There were distinct sediment belts: carbonate platforms of limestone and dolostone were widespread, close by were lagoonal shale and near-shore siliceous sandstone. On the outer shelf, carbonates graded seaward into deep-shelf and continental-slope shale. Outer-shelf and inner-shelf environments were isolated due to elevated temperature and salinity. Inner-shelf biotas were sparser and disarticulated. Outer-shelf biotas were abundant and highly diverse due to unrestricted water circulation and normal salinity conditions (Robison et. al., 2015).

The Wheeler and Marjum formations were named from type localities in the House Range of west-central Utah. The Wheeler ranges up to 300 m in thickness and was deposited in a deep, asymmetrical sea-floor trough called the House Embayment (Rees, 1986). It deepened (present-day) westward and extended more than 400 km diagonally northeastward into the carbonate platform. The trough was likely a seafloor escarpment formed by displacement along a fault, possibly related to earlier tectonic separation of Siberia and Laurentia (Robison et. al., 2015).

The Poleta Formation was deposited in the Esmeralda Basin, on the margin of Laurentia (Hollingsworth, 2005). The Montezuma Range is located in the Esmeralda Basin, with Indian Springs Canyon to the east side. The Indian Springs Lagerstätte was deposited in an off-shore shelf setting that was subject to storm-initiated sediment pulses. The Montezuma Range is part of the Basin and Range Province. Faulting, folding, and volcanic cover are frequent in the Montezuma Range and often obscure stratigraphic sections. The Poleta is up to 125 m thick in Indian Springs Canyon. The Poleta Formation can be traced from the Montezuma Range westward into the White–Inyo Mountains of California, and southward into Death Valley and the Mojave Desert (English and Babcock, 2010).

The Kinzer Formation was deposited on the edge of the carbonate platform developing on eastern Laurentia. The Octararo lay between this margin and island microcontinents, Baltimore and Brandywine. This could represent a failed rift or a volcanic island arc (Skinner, 2005).

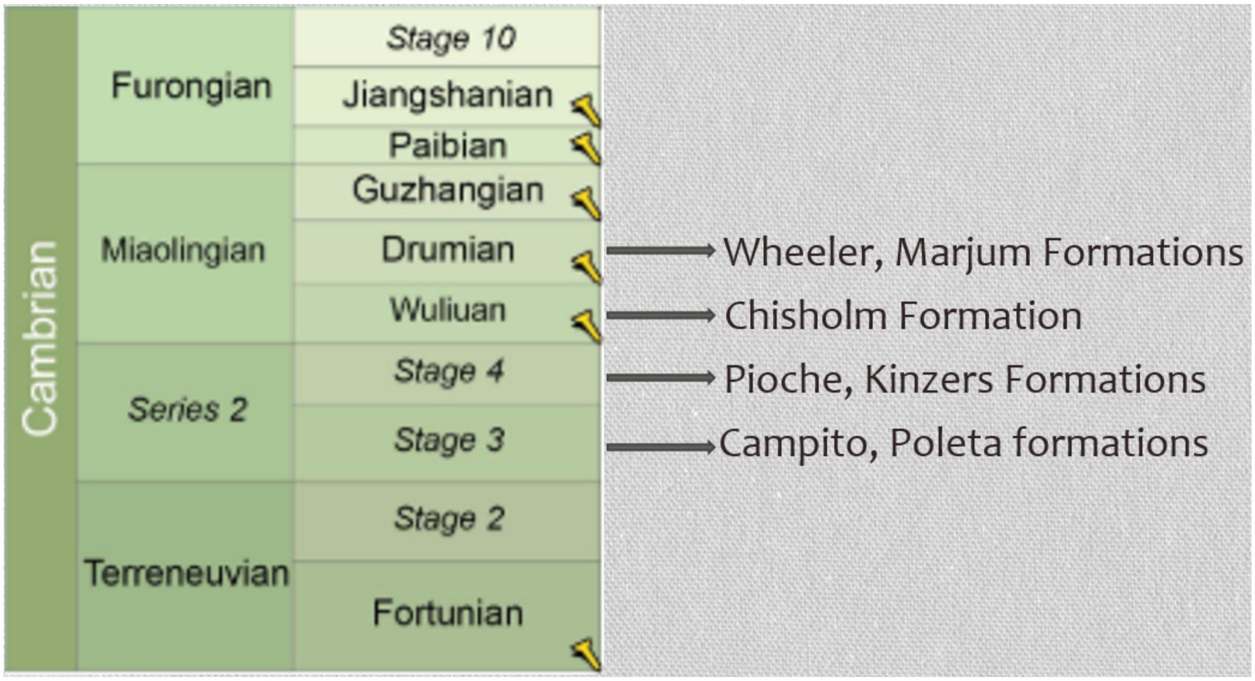

Figure 2. Cambrian section of the stratigraphic column showing the age of each formation.

METHODS

This work represents a revision of criteria earlier established by Babcock and Robinson (1989) and Babcock (1993) for injuries to trilobites, and by Zangerl and Stanley (1963) for coprolites and cololites. As revised here, damage to trilobite exoskeletons can be categorized according to the criteria listed below.

Specimens were studied using a Wild M5A microscope.

A FEI Quanta 250 field emission gun scanning electron microscope (SEM) at the Subsurface Energy Materials Characterization and Analysis Laboratory (SEMCAL), School of Earth Sciences, The Ohio State University for further study of some specimens. Studied specimens were left uncoated.

Specimens were counted and categorized according to flow charts that were developed. This was further broken down by species within a formation and location of the breakage on the trilobite. These numbers are also compared to the number of undamaged trilobites.

Data on approximately 340 species are reported below.

Criteria used for categorizing damage to trilobite exoskeletons are presented here as an outline to facilitate recognition. It is designed to be read as a key, using either-or choices. Most choices are followed by criteria used for diagnosis

1. Healed Injuries

Criteria:

-Breakage of the exoskeleton

-Occur on pleural lobes

-possible deformed or thickened exoskeleton in damaged area

1.1. Predation Scars
Criteria:

- Scars on posterior of the body are likely indicators.
- On areas not likely to be accidentally injured.
- Predation scars are commonly arcuate to asymmetrically W-shaped.

1.2. Injuries of Uncertain Origin
Criteria:

- Areas most susceptible to accidental damage are spines, facial sutures, and margins between the dorsal exoskeleton and the doublure.
- Simple straight, slightly curved, or jagged breaks as might be expected from some types of accidental breaks.

2. Scavenging Remains

2.1 From either corpses or molts.

2.2 Corpse

Criteria:

- Sclerites are disrupted and/or fragmented.
- Fossilized gut, indicating a corpse, present or absent.

2.3 Molt

Criteria:

- If legs are not present, likely a molt.
- Sclerites are disrupted and/or fragmented.
- Fossilized gut, indicating a corpse, present or absent
- Dislocated free cheeks.
- Lack of preserved gut.
- Cephalon absent (in some).

3. Lethal Predation Injuries

Criteria:

- Fossilized gut likely present. (Crushed glabella, early mineralized gut tract.)
- Fragmented/broken sclerites, disrupted sclerites.
- Breakage of the axial lobe likely.

4. Coprolites

Criteria:

- Sclerites present inside an elongate or ovoid mass.
- Sclerites of echinoderms, brachiopods may be present.
- Groundmass is light brown to dark brown to black.
- No structure in thin section.
- Groundmass greatly exceeds inclusions in volume.
- Often a peripheral layer of sulfides and sulfates.

4.1. Irregular Compact Form

Criteria

- Groundmass is not homogenous.
- Groundmass is transected by small cracks filled with calcite.

4.2. Trains/Splatters

Criteria:

- Contain irregularly shaped tufts of fecal groundmass strewn across shale.

5. Gut Contents/Cololite

Criteria:

- Sclerites present inside a predator's gut tract.
- Sclerites of echinoderms, brachiopods may be present.

5.1 Ejected prey
Criteria:

- Whole or partial skeletons are disarticulated and disoriented.
- Head, thoracic section, and tail still in proper spatial relationship.
- Small tufts resembling groundmass of coprolites.
- Surfaces of skeleton are bright.

5.2. Gastric residues

5.2.1. Loosely-strewn

Criteria:

- ➢ Skeletal components are intermingled and splattered.
- ➢ Characteristic pattern: small area densely aggregated, and density sharply decreases outward.
- ➢ Symmetrical or fans off.

5.2.2. Pellet shaped

- ➢ Can't be distinguished from coprolites.
- ➢ Thick masses of skeletal debris in a brown groundmass.
- ➢ Uniform mass.

6. Disaggregated/Fragmented Sclerites

6.1. Disaggregated fecal remains
Criteria:

- Some are fragmented. No obvious coprolite shape.
- Scattered on bedding plane.
- Sclerites of echinoderms, brachiopods may be present.

6.2.Disaggregated Sclerites of Uncertain Origin
Criteria:

- Unfragmented. Scattered on bedding plane.
- Sclerites of echinoderms, brachiopods may be present.

7. Exoskeleton without healed injury, lethal injury, or evidence of scavenging.

Results

Examples of damage to trilobite exoskeletons are illustrated in Figures 3–5. Figures 3 and 4 show specimens having sublethal bite marks, and Figure 5 shows an example of a scavenged trilobite.

Figure 3. 5 cm specimen of Elrathia kingii from the Cambrian of Utah showing sublethal predation scars on the right thorax.

Figure 4. 4 cm specimen of Elrathia kingii from the Cambrian of Utah showing sublethal predation scars on the right thorax.

Figure 5. 3 cm Specimen of Alokistocare harrisi from the Cambrian of Utah showing disrupted thoracic segments due to scavenging.

Qualitative Data

Overall Pattern: More than 400 specimens were examined. Evidence of lethal predation, as a percentage of the total number of trilobite fossils, is greater in the Campito, Poleta, and Pioche formations, compared to the Wheeler and Marjum formations. Sublethal injuries are more common in the Wheeler and Marjum formations, although separated or broken sclerites are the most common trilobite fossils in these units. Few specimens were examined from the Kinzers and Chisholm formations.

Campito Formation: The greatest amount of unhealed bites, as a percentage of total injuries studied, are in this formation. The Campito Formation is significantly different from the other formations studied in that it few studied specimens were complete, articulated exoskeletons. It mostly contains severely fragmented trilobites which can be difficult to discern from one another.

Poleta Formation: Few complete specimens were studied from this unit. Cephala were commonly separated from other sclerites, and sometimes broken. Thoracic segments were commonly disrupted. For the most part in this study, specimens consisted of broken sclerites, compared to the total percentage of injuries studied.

Pioche Formation: Many specimens are disarticulated, as shown in Figures 6 and 7.

Figure 6. Disarticulated cephalon from the Pioche Formation.

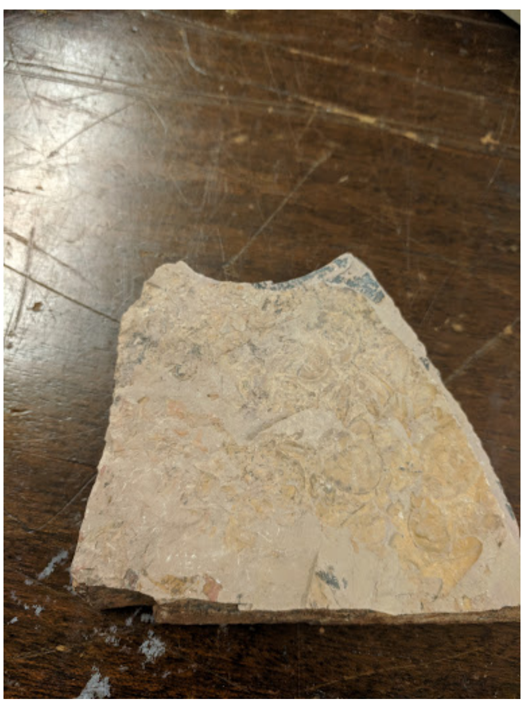

Figure 7. Disarticulated cephala and sclerites from the Pioche Formation.

The cephala are separated from the thorax. Some have clear healed or unhealed bite marks. Some are disturbed or scavenged; thoracic segments are commonly removed, tipped over, or broken. One cephalon bitten in half was studied. Some specimens are undisturbed complete exoskeletons. There are many chewed specimens, but overall, more complete exoskeletons were observed in this study from this formation compared to the Poleta Formation.

Kinzers Formation: Injuries are rare, as a percentage of the total number of studied injuries by formation.

Marjum Formation: It is easy to distinguish between corpse and molt: a missing free cheek indicates a molt, and the presence of fossilized gut is unambiguous evidence of a corpse. There is little evidence of scavenging in the studied specimens, as a percentage of total studied specimens.

Wheeler Formation: Corpses and molts can be easily distinguished: a missing free cheek indicates a molt, and the presence of fossilized gut is unambiguous evidence of a corpse. There is little evidence of scavenging in the studied specimens, as a percentage of total studied specimens.

Quantitative Data

Figures 8–10 illustrate the quantitative results on damaged trilobite exoskeletons. Figure 8 shows the overall results, Figure 9 results for one formation (the Campito Formation), and Figure 10 shows results for one species (*Elrathia kingii*).

Overall Pattern: The overall pattern is based on the total number of specimens counted, 340, showing predation scars and breakage by scavenging, except for those from the Campito Formation. For predation scars, there was one specimen with a scar on the left cephalon, one specimen with a scar on the left anterior thorax, 2.5 specimens with a scar on the right anterior thorax, 11 specimens with scars on the left posterior thorax, and 23.5 specimens with scars on the right posterior thorax. For scavenging, there were 2 specimens with scavenging on the left cephalon, 1 specimen with scavenging on both sides of the cephalon, 0.5 specimens with scavenging on both sides of the anterior thorax. 9.5 specimens with scavenging on both sides of the posterior thorax, and 4 specimens with scavenging on the posterior thorax. One note: numbers ending in a decimal (example, 0.5) indicate that a specimen was counted entered into the data set for two types of injuries. Also note that the anterior thorax was defined as the first three thoracic segments.

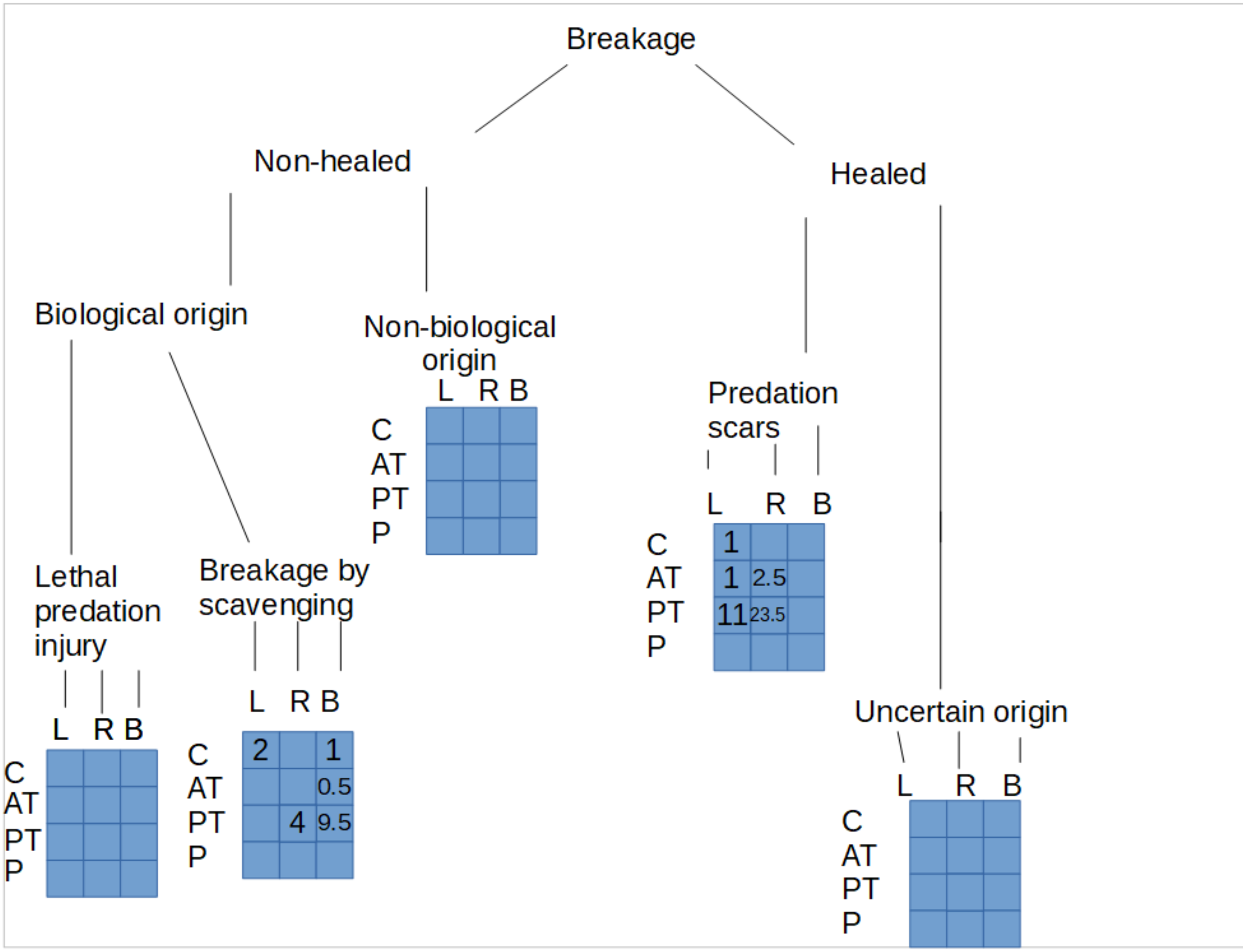

Figure 8. Data on the location of injuries on trilobites from the Cambrian of North America illustrate use of the criteria for determining the origin of injuries.

Campito Formation

-*Esmeraldina*: 62 specimens were studied in total. Isolated cephala are most common in the studied specimens, with 51 specimens displaying them. There were also 5 specimens with broken isolated cephala, 3 specimens with cephala and partial thorax, 2 specimens with healed injuries and a broken cephalon, and one specimen with a partial thorax.

-*Nevadia*: 49 specimens were studied in total. Broken isolated cephala, 14 specimens, and isolated sclerites, 15 specimens, are most common in the studied specimens. There are also 11 specimens with isolated cephala, 4 specimens with a cephalon and a partial thorax, one specimen with a thorax and pygidium, one specimen with healed injuries and a broken cephalon, one complete specimen, and 2 specimens with a partial thorax.

	Nevadia	Esmeraldina
Isolated Cephla	11	51
Isolated Cephla, broken	14	5
Cephalon and partial thorax	4	3
Thorax and Pygidium	1	
Isolated Sclerites(Broken and a lot)	15	1(at least 4 cephala)
Healed injuries(also broken cephalon)	1	2
Complete	1	
Partial thorax	2	1

Figure 9. A sample of trilobites from the Cambrian of Nevada illustrates the use of the criteria for determining the origin of injuries. The Campito Formation is a difficult formation to examine but the criteria has assisted in better distinguishing between injury types. Isolated cephala, isolated sclerites, broken pieces, and jumbled masses of fragments are common in this formation.

Pioche Formation:

-*Olenellus brevispinus* displays one specimen with scavenging on both sides of the anterior and posterior thorax.

-*Olenellus gilberti* displays 2 specimens with scavenging on the left cephalon and 5 specimens with scavenging on the left posterior thorax. 7 specimens were examined in total.

-*Olenellus geniculatus* displays one specimen with scavenging on the left posterior thorax.

-*Olenellus fowleri* displays one specimen with scavenging on the left posterior thorax.

-*Olenellus chiefensis* displays one specimen with scavenging on the left posterior thorax.

Kinzers Formation:

-*Olenellus thompsoni* displays two uninjured trilobites.

Chisholm Formation:

-*Glossopleura sp.* displays one healed injury on the left posterior thorax.

Marjum Formation:

-*Modocia laevinucha* displays one specimen with scavenging on the entire cephalon, one specimen with scavenging on the right posterior thorax, one specimen with predation scars on the left posterior thorax, and 55 uninjured specimens. 58 specimens were examined in total.

-*Modocia typicalis* displays on specimen with predation scars on the left cephalon.

Wheeler Formation:

-*Elrathia kingii* displays one specimen with predation scars on the left anterior thorax, 2.5 specimens with predation scars on the right anterior thorax, 9 specimens with predation scars on the left posterior thorax, 22.5 specimens with predation scars on the right posterior thorax, and 14 uninjured specimens. 48 specimens were examined in total.

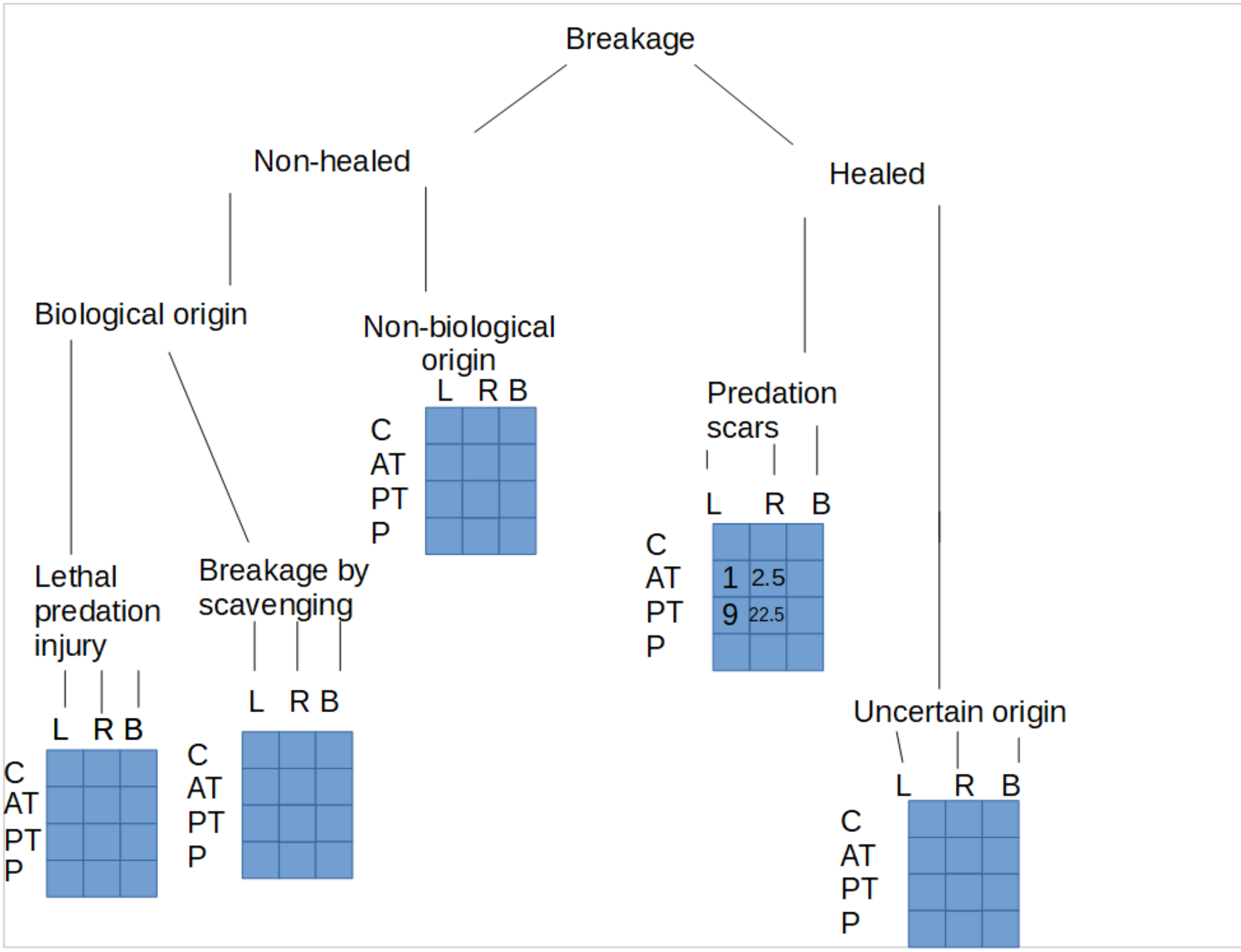

Figure 10. A sample of trilobites from the Cambrian of Utah illustrates the use of the criteria for determining the origin of injuries. In Elrathia kingii, there is a strong tendency for injuries to be on the right posterior thorax.

-*Asaphiscus wheeleri* displays one specimen with scavenging on the right posterior thorax and one specimen with a predation scar on the right posterior thorax. Two specimens were examined in total.

-*Alokistocare harrisi* displays 2 specimens with scavenging on the right posterior thorax and one specimen with scavenging on the entire posterior thorax. 3 specimens were examined in total.

SEM images

Certain specimens were studied further with a Scanning Electron Microscope (SEM). This allowed for detailed study of the evidence of regeneration (Figure 11). One specimen studied shows a clear image of the gut, which represents unambiguous evidence of a corpse (Figure 12).

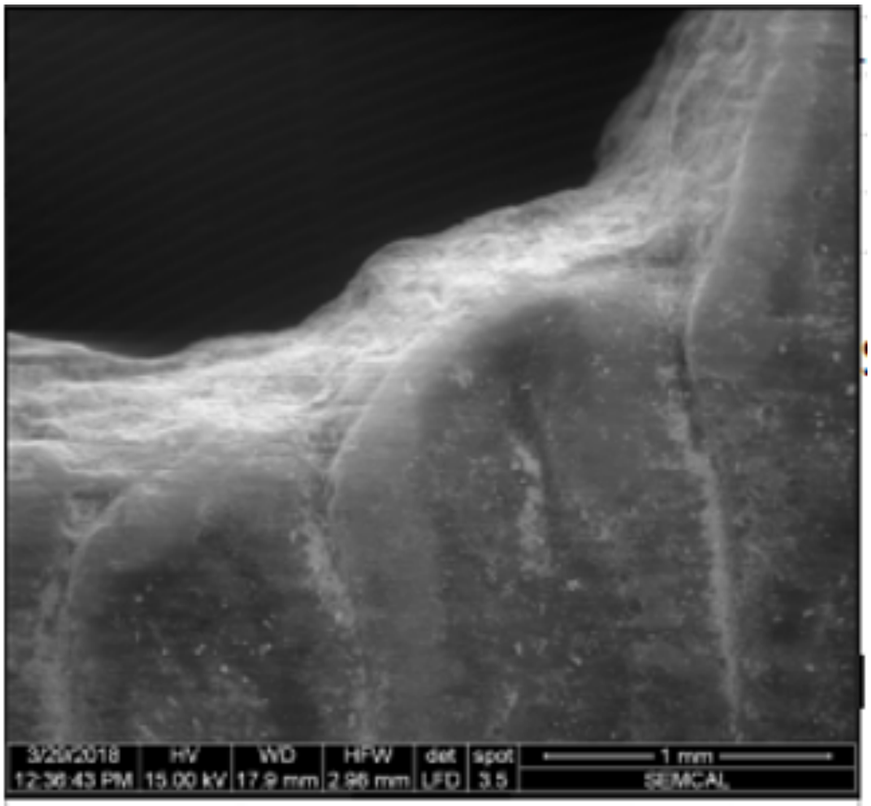

Figure 11. Scanning Electron Microscope (SEM) reveals details of healed sublethal injuries. This image, from the right thorax of an Elrathia kingii, shows scarring and partial regeneration of the tips of the thoracic segments.

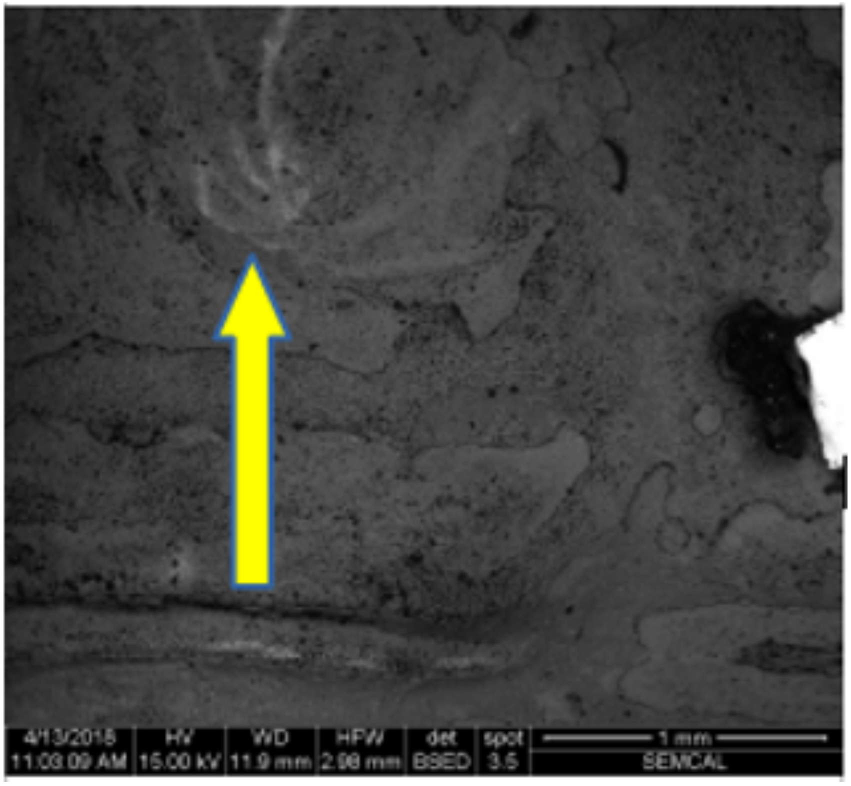

Figure 12. Scanning Electron Microscope (SEM) reveals the gut of a trilobite. This is a clear indicator of a corpse.

Discussion

Clarification of the criteria, discussed in methods, used to analyze broken trilobite exoskeletons, successfully facilitates distinguishing the origins of breakage. Sublethal predation scars are recognized by an arcuate to asymmetric w shape and occurring on areas not likely to be accidentally injured. Lethal predation injuries scars are recognized by fragmented or broken sclerites, and breakage of the axial lobe. Injuries of uncertain origin include spines, facial sutures, and other areas that are more susceptible to accidental damage. The breaks are straight, slightly curved, or jagged, indicating accidental injury. Most observed injuries fall into the category of sublethal predation scars. In the following paragraphs, specific patterns of damage to trilobite exoskeletons are summarized.

The overall pattern is based on the total number of specimens counted, 340, showing predation scars and breakage by scavenging, except for those from the Campito Formation. For predation scars, there was one specimen with a scar on the left cephalon, one specimen with a scar on the left anterior thorax, 2.5 specimens with a scar on the right anterior thorax, 11 specimens with scars on the left posterior thorax, and 23.5 specimens with scars on the right posterior thorax. For scavenging, there were 2 specimens with scavenging on the left cephalon, 1 specimen with scavenging on both sides of the cephalon, 0.5 specimens with scavenging on both sides of the anterior thorax. 9.5 specimens with scavenging on both sides of the posterior thorax, and 4 specimens with scavenging on the posterior thorax. Commonly, predation is heavy in the Pioche, Campito, and Poleta formations, compared to the Marjum and Wheeler formations.

Specimens from the Wheeler and Marjum formations show little evidence of scavenging, as a percentage of total studied injuries. It is easy to distinguish between a corpse and a molt for these formations, indicated, for example, by missing free cheeks. Specimens of Elrathia kingii from the Wheeler Formation show significant numbers of sublethal predation scars, as compared to the total percentage of scars. There appears to be a preference for unhealed injuries to be preserved on the right thorax. This suggested that areas in other locations were either less common or fatal. This preliminary evidence seems to suggest more efficient predator-resistant structures or behavioral strategies.

The Chisholm and Kinzer formations show less preservation of healed bite marks in general compared to the other formations in this study.

The Pioche Formation indicates significant scavenging with few sublethal predation scars preserved, as a percentage of total injuries.

The Poleta and Campito formations show significant scavenging, lethal, and sublethal predation. In the case of the Poleta specimens, this results in not even being able to take a quantitative sampling. Whole trilobites are rarely displayed in these formations, but rather appear has isolated cephala, cephala bitten in half, broken pieces, jumbles of sclerites, and other pieces jumbled together. These are clear signs of successful predators.

CONCLUSIONS

The ease of analyzing the origins of breakage in trilobites was significantly increased by using the criteria presented in this thesis. Detailed study of sublethal breakage shows that trilobites had the capability of healing sublethal wounds by regenerating lost tissue during subsequent molt stages.

Most trilobites are represented by fragmented remains. In some deposits, injuries are relatively common. These instances were studied in greater detail. Overall, the specimens show that injuries of uncertain origin are rare. Many predators commonly macerated their prey, as shown by the fact that lethal predation injuries are rare as trace fossils on articulated specimens. Compared to the number of uninjured trilobites, injuries in general were rare, showing that Cambrian predators were more often successful than unsuccessful.

There appears to be considerable variability among species in the type of injuries preserved. Olenellines (Stage 3-Stage 4) had low incidences of preserved sublethal predation scars. Some Drumian Age taxa, such as Elrathia and Asaphiscus, had higher incidences of sublethal predation scars. Sublethal injuries on specimens of Elrathia kingii were preferentially preserved on the right thorax, which suggests that injuries in other areas were inflicted less often or more likely to prove fatal. Other common trilobites of the Drumian, such as Modocia, tend to have few preserved sublethal predation scars. Some trilobite clades may have evolved more efficient predation-resistant strategies through time, as this preliminary evidence seems to indicate. Lethal predation or scavenging is represented through the Cambrian Stage 3-Drumian interval by unhealed, broken sclerites, in coprolites, and in cololites. Incomplete, partly disrupted exoskeletons interpreted as scavenged remains are common in Cambrian Lagerstätten.

Recommendations for Future Work

These criteria can be applied to other projects on trilobites, or other arthropods, from anywhere. These general concepts can also be applied to other organisms. A project could be done to apply these criteria to other localities, such as The Columbus Limestone and Ohio Shale. There could also be a more comprehensive study done of applying the criteria to coprolites and cololites, in an attempt to better differentiate the two. In this research, it was not possible to determine for sure that certain specimens with detached sclerites were coprolites. It would be beneficial to have specimens that display a clear biofilm that could be examined according to the criteria. There also can always be more work to do on trying to better observe patterns of breakage for individual species. In this study, only *Elrathia kingii* displayed a pattern. It is likely that other species might to. There is also work to be done to further determine the reasons for *Elrathia kingii* displaying this pattern.

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APPENDIX

Injuries to trilobite specimens examined in this study.

	Lethal Predation Injury											
	LC	RC	BC	LAT	RAT	BAT	LPT	RPT	BPT	LP	RP	BP
116. Elrathia kingii												
115. Elrathia kingii												
116. Asaphiscus wheeleri												
114.Elrathia kingii												
115. Asaphiscus wheeleri												
115. Alokistocare harrisi												
Kinzers Formation Olenellus thompsoni												
Ruin Wash Olenellus brevispinus												
Ruin Wash Olenellus gilberti												
Ruin Wash Olenellus geniculatus												
Ruin Wash Olenellus fowleri												
Ruin Wash Olenellus chiefensis												
Chisholm Formation Glossapleura sp.												
382 Modocia laevinuch												
716 Modocia typicalis(also a growth)												
811 Modocia laevinucha(not many isolated bits and pieces)												
770 M. laevinucha												
Total												

	Scavenging											
	LC	RC	BC	LAT	RAT	BAT	LPT	RPT	BPT	LP	RP	BP
116. Elrathia kingii												
115. Elrathia kingii												
116. Asaphiscus wheeleri												
114.Elrathia kingii												
115. Asaphiscus wheeleri								1				
115. Alokistocare harrisi								2	1			
Kinzers Formation Olenellus thompsoni												
Ruin Wash Olenellus brevispinus						1			0.5			
Ruin Wash Olenellus gilberti	2								5			
Ruin Wash Olenellus geniculatus									1			
Ruin Wash Olenellus fowleri									1			
Ruin Wash Olenellus chiefensis									1			
Chisholm Formation Glossapleura sp.												
382 Modocia laevinuch												
716 Modocia typicalis(also a growth)												
811 Modocia laevinucha(not many isolated bits and pieces)			1					1				
770 M. laevinucha												
Total	2		1			1		4	9.5			

	Non-biologic origin											
	LC	RC	BC	LAT	BAT	RAT	LPT	RPT	BPT	LP	RP	BP
116. Elrathia kingii												
115. Elrathia kingii												
116. Asaphiscus wheeleri												
114.Elrathia kingii												
115. Asaphiscus wheeleri												
115. Alokistocare harrisi												
Kinzers Formation Olenellus thompsoni												
Ruin Wash Olenellus brevispinus												
Ruin Wash Olenellus gilberti												
Ruin Wash Olenellus geniculatus												
Ruin Wash Olenellus fowleri												
Ruin Wash Olenellus chiefensis												
Chisholm Formation Glossapleura sp.												
382 Modocia laevinuch												
716 Modocia typicalis(also a growth)												
811 Modocia laevinucha(not many isolated bits and pieces)												
770 M. laevinucha												
Total												

	Predation scars											
	LC	RC	BC	LAT	RAT	BAT	LPT	RPT	BPT	LP	RP	BP
116. Elrathia kingii				1				2				
115. Elrathia kingii					3		9	19.5				
116. Asaphiscus wheeleri								1				
114.Elrathia kingii								1				
115. Asaphiscus wheeleri												
115. Alokistocare harrisi												
Kinzers Formation Olenellus thompsoni												
Ruin Wash Olenellus brevispinus												
Ruin Wash Olenellus gilberti												
Ruin Wash Olenellus geniculatus												
Ruin Wash Olenellus fowleri												
Ruin Wash Olenellus chiefensis												
Chisholm Formation Glossapleura sp.							1					
382 Modocia laevinuch							1					
716 Modocia typicalis(also a growth)	1											
811 Modocia laevinucha(not many isolated bits and pieces)												
770 M. laevinucha												
Total	1				3		11	23.5				

	Uncertain origin												No injuries
	LC	RC	BC	LAT	RAT	BAT	LPT	RPT	BPT	LP	RP	BP	
116. Elrathia kingii													1
115. Elrathia kingii													13
116. Asaphiscus wheeleri													
114.Elrathia kingii													
115. Asaphiscus wheeleri													
115. Alokistocare harrisi													9
Kinzers Formation Olenellus thompsoni													2
Ruin Wash Olenellus brevispinus													
Ruin Wash Olenellus gilberti													3
Ruin Wash Olenellus geniculatus													2
Ruin Wash Olenellus fowleri													1
Ruin Wash Olenellus chiefensis													1
Chisholm Formation Glossapleura sp.													
382 Modocia laevinuch													6
716 Modocia typicalis(also a growth)													
811 Modocia laevinucha(not many isolated bits and pieces)													36
770 M. laevinucha													13
Total													87